FORAGING BEHAVIOR OF BUMBLEBEES ON FALSE FOXGLOVE

Edmund W. Stiles

There is a large body of recent literature exploring the theoretical aspects of foraging behavior (Emlen, 1966; Schoener, 1971; Pulliam, 1974; Krebs, Ryan and Charnov, 1975; Orians and Pearson, 1977). Field tests of these theoretical treatments are few, however, as the measurement of parameters to test predictions from theory is in many cases difficult. Bumblebees possess many characteristics which make them good subjects for foraging behavior studies including ease of field observation, quantifiable resource levels and abundance of individual foragers.

Foraging behavior in bumblebees may be analyzed by providing answers to four basic questions:

1. What types of food are used?

2. Where do bees forage or which resource patches do they select?

3. How long do the bees remain in a patch?

4. What are the patterns of speed and direction of movement within and between patches?

I will give a preliminary report on work examining aspects of speed and direction of movement of three species of bumblebees foraging on False Foxglove (*Aureolaria pedicularia*) in the New Jersey Pine Barrens.

Study Site and Methods

The study site was an Oak-Pine forest (McCormick and Jones, 1973) in Lebanon State Forest, New Jersey. This area is control-burned at least every third year and contains large stands of *Aureolaria pedicularia*. A 10 × 10 m grid was established in a large single-species stand of *Aureolaria* and grid squares were marked with numbered stakes. The number of flowers in each grid square was counted every morning.

Foraging was recorded by noting the species and sex of the bee, the time of day, the sequence of grid squares visited and the number of flowers within each square that was visited. For each flower visit I also recorded the activity of the bee at the flower, collecting nectar, collecting pollen, robbing, or any combination of these. The total time of an observation from when the bee was first sighted to the time the bee left the grid was also recorded.

Study Organisms

Aureolaria pedicularia (L.) Raf. is a much-branched annual reaching 1 m in height. In the New Jersey Pine Barrens it flowers from late August to late September bearing yellow, zygomorphic, campanulate flowers. The flowers are 3–4 cm in length and last for one day. Floral density during the one month study period reached as high as 1584 of these large flowers on the 10 × 10 m study grid. The flowers offer large quantities of pollen and nectar and are visited regularly by three common species of bumblebees.

The three species, *Bombus impatiens* Cresson, *B. vagans* Smith, and *B. affinis* Cresson, were common foragers on the grid being represented by both males and workers. Males of *B. vagans* were rarely found foraging on *Aureolaria*, using primarily other plant species in the area. The data for males of this species will be included even though sample size were low. *B. vagans* was the smallest of the three. *B. impatiens* was intermediate, while *B. affinis* was the largest species foraging on the grid.

Results

For the three species of bumblebees studied and for both males and workers I made the following computations:

1. The average time spent per flower, evaluating the speed of foraging while in the grid.

2. The total flowers visited divided by an index of the potentially available flowers. {If F_i = flower density in grid square i and D_i = the straight-line distance traveled by the foraging bee in grid square i, then the Index of Potentially Available Flowers = $\sum(F_i \times D_i)$}.

3. The total distance traveled within the grid divided into the straight-line distance from the point of first observation of the bee to the point of exit from the grid. This evaluates the degree of curvature of travel of bees foraging in the grid. A value of 1.0 would mean the bee traveled in a straight line.

All foraging observations which I will use here to compare species foraging behavior are of bees robbing nectar. By 10:00 AM virtually all the flowers that had opened that morning had holes cut in the base of the corolla tubes which the bees used for robbing nectar. The largest species, *B. affinis*, is a primary nectar robber and cut holes in the bases of the corolla tubes to obtain nectar. A soldier beetle, *Chauliognathus pennsylvanicus* DeGreer (Cantharidae), was also common on the flowers and was also a primary nectar robber. The other two species of bumblebee did not cut holes in the flowers, but used the holes freely to obtain nectar after they

Table 1. Speed of movement as the average number of seconds spent per flower visited, Path Width as the flowers visited divided by an index of potentially available flowers and Curvature as the straight-line distance from first observation to leaving the grid divided by the total distance traveled for three species and two sexes of bumblebees.

	Bombus impatiens		*Bombus vagans*		*Bombus affinis*	
	♀	♂	♀	♂ *	♀	♂
Speed	7.6	7.4	6.8	2.6	6.5	5.7
Path Width	.20	.18	.22	.21	.27	.19
Curvature	.19	.22	.35	.37	.38	.42

* Sample size inadequate.

had been cut. The observations compared here are of similar foraging behaviors in the three species.

Speed of foraging was slower for *B. impatiens* than for the other two species (Table 1). The number of seconds spent per flower includes the time spent on the flower plus the time spent flying to the next flower. Time in flight, however, was small relative to the time spent on the flower and the difference reflects the difference in feeding behavior on the flowers. In all three species, the males foraged faster than the workers. Additional data, however, will be needed to substantiate the difference in foraging speed in *B. impatiens*.

An evaluation of foraging path width was made by dividing the number of flowers visited by the index of potentially available flowers. Of the workers of the three species, *B. affinis* visited the widest path, *B. vagans* the next widest and *B. impatiens* the narrowest. In comparison with workers, males of all three species foraged using narrower paths (Table 1).

The curvature of flight path was measured for all species. *B. impatiens* workers showed the greatest degree of path curvature having almost twice that of *B. affinis* workers. Males for all species showed lower degrees of curvature than workers of the same species (Table 1).

Discussion

The behavioral difference among the three species and two castes of bumblebees are being analyzed in greater detail and the temporal analysis of changes in behavior with changing flower densities will be presented elsewhere. The implications that surface from the information presented above are applicable to the theory of central-place foraging (Orians and Pearson, 1977). Central-place foragers search for resources which they bring to some central place to store or feed young. The travel parameter in

the optimal foraging equation (see Schoener, 1971, for review) is of greater importance than for a non-central-place forager. In light of this, bumble-bees make excellent subjects with which to compare central-place and non-central-place foraging for worker bumblebees are central-place foragers and male bumblebees are not.

Movement away from the central place, or nest, is important for the central-place forager because of the energy necessary for the return trip with a load of food. One can predict that there should be selection to modify foraging behavior to minimize return traveling distance in worker bumble-bees. Optimal foraging theory without central-place foraging constraints would predict that straight-line movement would, on the average, result in more energy per unit time for a foraging bee due to the reduced probability of visiting the same flower twice. Central-place foraging predicts, however, that the worker bee should either travel in a more curved path or visit a wider path of flowers within a patch or both. These behavioral modifications will reduce the distance moved away from the central place for the same number of flowers visited.

Both the data on path width from measures of the flowers visited divided by the potentially available flowers and the data on the curvature of path support the prediction that workers, more than males, forage in a fashion that would reduce the energy necessary to return to a central place. Males of all three species exhibit use of narrower paths and have less curvature to their foraging paths when foraging through a grid of *Aureolaria pedicularia.*

This provides additional support for work done by Stiles on alder forest birds (in press) and G. H. Orians on Brewer's Blackbirds (personal communication) demonstrating the behavioral modifications of central-place foragers.

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Department of Zoology, Rutgers—The State University of New Jersey, New Brunswick, N. J. 08903.